

NOTES ON THE FRUIT ANATOMY OF AUSTRALIAN MEMBERS OF THE INULEAE (COMPOSITAE)

by

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ABSTRACT

Short, P. S., Wilson, K. E. & Nailon, J. Notes on the fruit anatomy of Australian members of the Inuleae (Asteraceae). *Muelleria* 7(1): 57–79 (1989). — Observations of the anatomy and morphology of Australian inuloid genera are presented. Genera examined include *Angianthus* Wendl. s. lat., *Helichrysum* Miller, *Helipterum* DC., *Ixiolaena* Benth., *Millotia* Cass., *Myriocephalus* Benth., *Podolepis* Labill., *Scyphocoronis* A. Gray and *Toxanthes* Turcz. Comments on generic delimitation are made.

INTRODUCTION

As an adjunct to revisionary studies (by Short) of Australian genera a study of the fruit anatomy and morphology of species of Inuleae was commenced in 1982. Initial studies involved an assessment of the value of fruit anatomy in ascertaining specific and generic limits, an assessment carried out through the study of the segregate genera of *Angianthus* Wendl. s. lat. previously recognized by Short (1983). Following encouraging results a more general survey was carried out.

It is clear from studies that fruit characters are of much value in ascertaining generic limits within the Inuleae, and descriptions of fruit are incorporated in revisions of *Blennospora* A. Gray (Short 1987), *Podotheca* (Short 1989) and *Pogonolepis* Steetz (Short 1986a). Forthcoming revisions of *Calocephalus* R. Br., *Gnephosis* Cass. and *Chthonocephalus* Steetz (all *sensu* Benth. 1867) will also include descriptions of the fruit anatomy of many of the segregate genera that will be recognized. In this paper results of the studies of *Angianthus* s. lat. and miscellaneous observations of other inuloid genera are presented.

MATERIALS AND METHODS

The extent of the observations of the fruit anatomy and morphology of species in this paper vary considerably. In some cases anatomical comments are the result of the examination of median-transverse sections (TS) and median-longitudinal sections (LS) of fruit, in others only TS have been studied. Similarly not all species have been examined with a scanning electron microscope (SEM), surface features sometimes being only examined by light microscope using a 40× objective. The bracketed abbreviations LS, TS & SEM accompanying the generic headings below are used to indicate the extent of observations.

Voucher specimens are housed in either AD or MEL, the majority being in the latter herbarium. The appendix lists the specimens examined, giving species name, author citation and collector's name and number.

Immature fruit were fixed in the field in 4:3:1 (chloroform: absolute ethanol: glacial acetic acid) and subsequently stored in 70% ethanol. Mature, dry fruit were rehydrated and then fixed in 5% glutaraldehyde in 0.03 M Pipes buffer. Following fixation and dehydration both immature and mature fruit were infiltrated with G.M.A., Spurr's or L. R. White (London Resin Co.). Infiltration of L. R. White over several weeks, with repeated two hour vacuum infiltrations, proved to be the most effective. Two micron thick sections were stained with toluidine blue (pH 4.5) and mounted in histomount.

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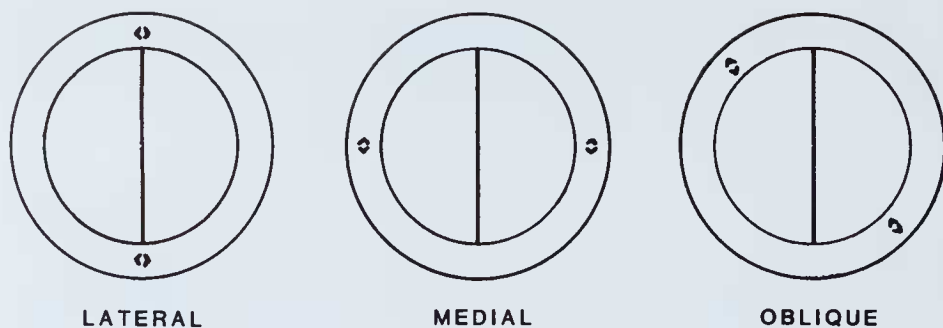


Fig. 1. The position of the vascular bundles in the pericarp in relation to the cotyledons.

To assist in the identification of vascular bundles in the pericarp fruit were cleared and stained in a solution of 1% basic fuchsin in 10% KOH (Wilcox 1977).

Terminology is generally self-explanatory and follows Bruhl (1984); the terms lateral, medial and oblique have been used to indicate the position of the vascular bundles in the pericarp and testa in relation to the cotyledons. In fruit with lateral vascular bundles the bundles occur in the plane of the upper surface of the cotyledons. In fruit with medial vascular bundles the bundles are opposite the lower surface of the cotyledons. If the position is intermediate between lateral and medial then bundles are considered to be oblique (Fig. 1). Placing the position of the bundles into one of the three categories did not usually present a problem. However, in some species any two bundles in a fruit were not opposite one another as illustrated in Fig. 1, but occupied different positions, e.g. one in a lateral position, the other in an oblique position. In a few species bundle position could not be determined as individual seedling leaves could not be discerned.

RESULTS AND DISCUSSION

GENERAL

Fruit anatomy, and to some extent morphology, has been generally ignored in taxonomic work in the Australian Asteraceae. A notable exception is the recent work on the *Cotuleae* (Bruhl 1984; Bruhl & Quinn 1988). Such studies are useful in deciding generic limits, a fact underlined by studies of most genera examined in this paper. This conclusion, plus the comments made below on the affinities of species and generic limits have been only reached following consideration of numerous morphological features of the taxa under discussion, not just fruit characteristics.

Fruit characteristics which are often indicative of species groups are:

- presence or absence and structure of thick-walled tissue in the pericarp and/or testa, e.g. compare *Helipterum albicans* with other species of *Helipterum*.
- presence or absence of a carpopodium, e.g. compare *Cephalosorus* and *Dithyrostegia* with other members of *Angianthus s. lat.* (also see Haque & Godward 1984).
- structure of the epidermis including trichomes, e.g. compare *Cephalosorus* and *Pogonolepis*, with fruit virtually enveloped in myxogenic cells, with other members of *Angianthus s. lat.*
- a crystalline pericarp, e.g. see *Craspedia*. Crystals are commonly found in the testa of most, if not all, inuloid species examined but not in the pericarp.

The presence or absence of vascular bundles in the testa may also be indicative of species groups, e.g. compare *Podolepis georgei* with other species of *Podolepis s. lat.* However, the reliability of our data is open to question. We stress that our observations of vascular bundles in the testa were only made from medial transverse sections. Ideally, cleared seed should be examined. Paul Wilson (pers. comm. 1988), following examination of cleared specimens, has recorded different results to us for

Table 1. Fruit characteristics in species of *Helipterum*.

(+ = present; - = absent or not applicable; L = lateral; M = medial; Ob = oblique; ? = number of vascular bundles not clear or position not known because cotyledons absent from section; () * = number of vascular bundles observed in cleared fruit (see text, p. 59).

	Layer of collenchyma or sclerenchyma in pericarp	Number of vascular bundles in pericarp in TS	Position of vascular bundles in pericarp	Number of vascular bundles in testa in TS	Position of vascular bundles in testa	Lateral thickening of epidermal cell walls
<i>H. albicans</i>	+	2	L	0	-	-
<i>H. charsleyae</i>	+	2	Ob	2	Ob	-
<i>H. chlorocephalum</i>	-	2	M	1	M	-
<i>H. floribundum</i>	-	2	?	1	?	-
<i>H. maryonii</i>	-	2	Ob/M	0(1)*	-	-
<i>H. microglossum</i>	-	2	?	1(?)	?	?
<i>H. moschatum</i>	-	2	M/Ob	0(1,2)*	-	+
<i>H. pygmaeum</i>	±	2	M	1(?)	M	+
<i>H. strictum</i>	-	2	Ob	2	Ob	-
<i>H. stuartianum</i>	-	2	M	0	-	-
<i>H. uniflorum</i>	-	2	Ob	0(1)*	-	+

some species of *Helipterum* (see Table 1). He has also recorded the presence of a vascular bundle in the testa of *Triptilodiscus*. We observed none in TS. The discrepancy in the data partly reflects the occasional difficulty in recognizing bundles in TS. However, it also reflects variation in the location of vascular bundles and the extent of vascularization in the testa. Observations by Paul Wilson indicate that a single vascular strand enters the testa through the funicle and penetrates a varying distance into the testa. Very often strands do not reach the apex of the ovule and the extent to which strands penetrate the testa may also vary within the one species. On entry to the ovule the strand may remain undivided or divide into two.

The position of the vascular bundles in the pericarp or testa is rarely constant in any species group, e.g. in *Angianthus s. str.* On the other hand, in *Podothea s. str.* only oblique bundles occur in the pericarp of the five species examined (Short 1989).

The possible occurrence of a reticulate venation pattern in the pericarp has been alluded to for *Craspedia* aff. *pleiocephala*. Of all species included in the general survey, including species in genera under revision and not included here, only *Gnephosis gynotricha* Diels definitely has reticulate venation. This pattern is absent from its close relative *G. macrocephala* Turcz.

In some species it was difficult, from transverse sections, to differentiate with certainty the testa from the pericarp. Sometimes this problem was overcome through the examination of sections of immature fruit. With many sections a clear gap exists between the layers of tissue considered to be testa and pericarp but in some species the tissue layers are all but obliterated in mature fruit. Thus it is possible that mistakes have been made in our interpretation of these tissues. Paul Wilson (*in litt.* 1987) has noted that, in *Blennospora*, a layer of sclerenchyma previously deemed to be in the pericarp (Short 1987) is more likely to be the outer layer of the testa. However, although the correct elucidation of testa and pericarp is critical for broad comparisons of composite genera, it is not so important for discerning species groups within unnatural genera. Differences in characters such as the presence or absence of sclerenchyma in the combined fruit/seed wall and the total number of vascular bundles are still useful features for indicating species affinities.

ACTINOBOLE Fenzl ex Endl. (LS, TS, SEM)

Fruit sections were obtained for each of the four species recognized in the genus (Short 1985). They are seemingly identical. All possess a prominent stylopodium, lack a distinct carpodium, are covered with twin-myxogenic hairs, and have two oblique vascular bundles in the pericarp. Vascular bundles are lacking from the testa (Figs 2a-b, 5d).

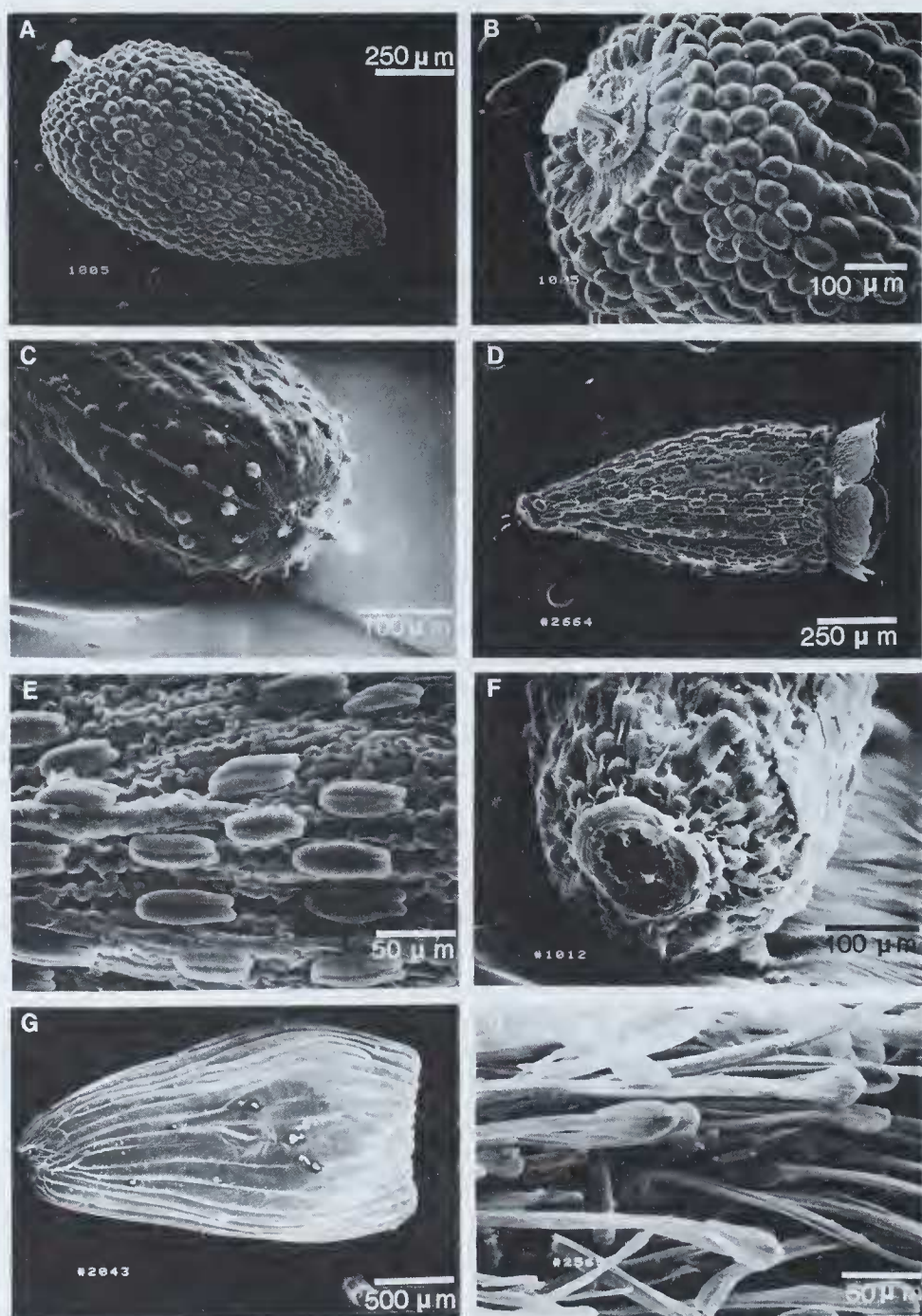


Fig. 2. Surface features of fruit. a, b — *Actinobole condensatum*, general view and apex showing the prominent stylopodium (Short 1005). c — *Angianthus acrohyalinus*, upper half of fruit with the position of the vascular bundle visible (Short 1000). d, e — *Angianthus* aff. *micropodioides*, general view and myxogenic hairs (Short 2664). f — *Angianthus* aff. *milnei*, carpodium (Short 1012). g — *Cephalosorus carpesioides*, general view (Short 2043). h — *Chondropyxis halophila*, trichomes (Short 2565).

ANGIANTHUS Wendl. *s. lat.*

In a recent revision (Short 1983) of *Angianthus s. lat.* eight genera were reinstated. Genera were recognized on the basis of a number of characters, including leaf morphology and the number, arrangement and morphology of the bracts of both the general involucre and capitula. Fruit characteristics were also used but additional notes on fruit structure are reported here.

Angianthus Wendl. *s. str.* (TS, SEM)

Species of *Angianthus* have a thin pericarp containing no thick-walled tissue. In all species it is difficult to differentiate the testa from the pericarp. In some sections a more or less well-defined, one-cell wide layer could be discerned. The cells have slightly thickened walls and it is probably the outer layer of the testa. Vascular bundles were not observed in the testa but two occur in the pericarp. The vascular bundles are oblique in *A. cunninghamii* and *A. acrohyalinus* but in *A. drummondii* they are almost medial. In both *A. brachypappus* and *A. milnei* one vascular bundle is in the lateral position, the other is oblique. Due to the thinness of the pericarp the position of the vascular bundles is often visible on the fruit surface as a small ridge (Fig. 2c). A carpopodium is well developed in all species (Figs 2d, f), and apparently twin-celled, myxogenic papillae occur on the fruit surface of most species (Figs 2c-f).

Cephalosorus A. Gray (LS, TS, SEM)

Cephalosorus is a monotypic genus. Fruit of *C. carpesioides* have an outer layer of myxogenic cells (Figs 2g, 5c). Two, more or less lateral vascular bundles occur in the pericarp. Vascular bundles were not observed in the testa, and thick-walled tissue is absent from both the testa and pericarp. A carpopodium is absent or poorly developed with the dehiscence region being in a pronounced basal hollow due to the large, myxogenic cells enveloping the fruit.

Dithyrostegia A. Gray (SEM)

Dithyrostegia contains two species, *D. amplexicaulis* and *D. gracilis* P. Short. Unlike all other species once referred to *Angianthus s. lat.* both have fruit enveloped by elongate, somewhat rigid hairs (Figs 3a, b). A carpopodium is absent.

Epitriche Turcz. (LS, TS, SEM)

Fruit of the only species, *E. cuspidata*, was not closely examined before the mounted sections had considerably faded. However, longitudinal sections revealed an unusual feature, that of a several cell-wide cap of sclerified tissue at the apex of the fruit. The pericarp, of which the cap is part, was barely sclerified in the TS of the fruit.

Hyalochlamys A. Gray (TS)

Hyalochlamys globifera A. Gray, the only member of the genus, has a more or less obpyriform, glabrous fruit with a well developed carpopodium. The pericarp is thin, lacks thick-walled tissue and contains two vascular bundles.

Pleuropappus F. Muell. (TS, SEM)

Angianthus phyllocalymmeus was referred (Short *l.c.*), with some apprehension, to *Pleuropappus*. Not only does the species superficially resemble many species of *Angianthus s. str.*, but it also has four capitular bracts which are arranged in the same manner as in *Angianthus*. However, *Pleuropappus* can be distinguished by the fruit, which are oblique to the corolla tube, the oblique pappus, and the presence and arrangement of about four capitulum-subtending bracts. The oblique orientation of the fruit does not occur in any other member of *Angianthus s. lat.*, although this same feature is found in *Rutidosis* (see below).

Transverse sections of fruit show no major anatomical differences between *P. phyllocalymmeus* and members of *Angianthus s. str.* The fruit wall is thin and the two vascular bundles, which only occur in the pericarp, are oblique (Fig. 12c). A carpopodium is also well developed in *Pleuropappus*. These observations do not support the reinstatement of the genus.

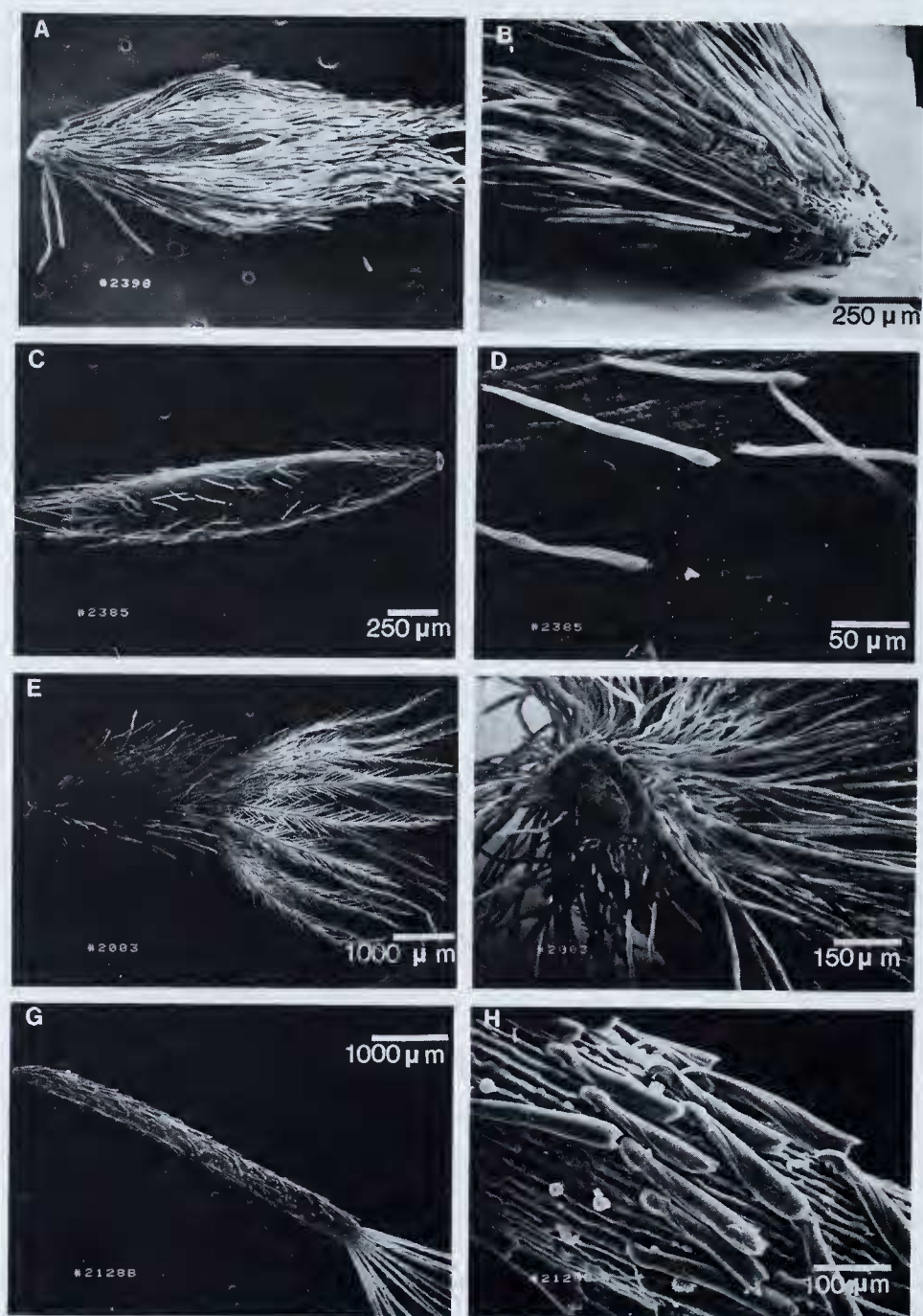


Fig. 3. Surface features of fruit. a,b — *Dithyrostegia amplexicaulis*, general view and base, note absence of carpodium (Short 2398). c,d — *Gnephosis pygmaea*, general view and trichomes (Short 2385). e,f — *Helipterum charasleyae*, general view and carpodium (Short 2003). g,h — *Millotia myosotidifolia*, general view and trichomes (Short 2128B).

Pogonolepis Steetz (LS, TS, SEM)

The outermost layer of the pericarp of species of *Pogonolepis* is composed of myxogenic cells (see Fig. 7, Short 1986a). There is also a pronounced carpodium. Layers of thick-walled tissue are absent from both the testa and pericarp. Two vascular bundles, more or less in the lateral position, occur in the pericarp (Fig. 10b). Vascular bundles were not observed in the testa. *Pogonolepis* and *Cephalosorus* are the only genera in *Angianthus s. lat.* to have species with the myxogenic cells covering the surface of the fruit. Despite this similarity they are not closely related, differing in many inflorescence and leaf characters.

Siloxerus Labill.

This genus, containing three species, was not closely examined for this paper. However, the cypselae are readily distinguished from those of other segregate genera by their colour alone. Beside the purple colour the small fruit are sparsely to densely papillose and lack a carpodium.

In the revision of *Angianthus s. lat.* (Short l.c.) three species, each clearly without close affinities with *Angianthus s. str.*, were treated as species of uncertain affinity. Each is now referred to a different genus, viz *Fitzwillia* P. Short, *Lemooria* P. Short and *Sondottia* P. Short (Short 1989). Fruit of *F. axilliflora* have some similarities with those in *Angianthus s. str.* in that in TS the fruit wall is thin, thick-walled tissue is lacking in either the testa or pericarp and there are two, oblique/medial vascular bundles in the pericarp. However, a carpodium is absent, a capping of sclerenchyma occurs at the fruit apex and the entire surface is covered with long, intertwined hairs. Fruit sections of *S. connata* (W. V. Fitzg.) P. Short have not been obtained. The fruit surface in this species is glabrous and there is a well developed carpodium. Fruit sections of *L. burkittii* faded before they were closely examined. Nevertheless it is evident that this species has two vascular bundles in the pericarp and that a few papillae are scattered over the fruit surface. Thick-walled tissue seems to be absent from the pericarp and testa.

CHONDROPYXIS D. Cooke (SEM)

Chondropyxis halophila was included by its author (Cooke 1986) in the Anthemideae but with the comment that, along with *Ceratogyne* Turcz., *Dimorphocoma* F. Muell. & Tate, *Elachanthus* F. Muell. and *Isoetopsis* Turcz. it formed a group with closer affinities to Astereae than Anthemideae. Bremer (1987) has suggested that *Isoetopsis* is a member of the Inuleae (subtribe Pluchinae). If this is the case then *Chondropyxis* possibly should be placed in the Inuleae. It is included in the current paper because of the distinctive hooked hairs which occur on the fruit (Fig. 2h), a form of trichome which does not seem to be widely distributed in the tribe.

CRASPEDIA Forst. f. (TS)

Fruit of two species currently included within *Craspedia* have been examined. One, Short 853, is a New Zealand member of the *C. uniflora* complex. The other species, Short 837, possibly *C. pleiocephala*, was collected in South Australia.

The New Zealand taxon has fruit with a thin pericarp (two cells wide) which lacks thick-walled cells and contains two vascular bundles in the lateral/oblique position. The testa lacks thick-walled tissue and vascular bundles were not observed. Externally the fruit are minutely papillate, occasionally have a sparse cover of long trichomes, and possess a prominent annular carpodium.

Craspedia aff. pleiocephala has two, oblique vascular bundles in the pericarp (Fig. 5a). Two to three scattered vessels were observed in some sections suggesting the presence of a reticulate venation system. However, the most striking aspect of this species was the presence of large, usually more or less oblong crystals in the pericarp. The crystals are not scattered but make up much of the pericarp, cell detail being obscured. Externally the fruit are silky hairy and lack a prominent, annular carpodium.

Craspedia, as currently delimited, is a heterogeneous group. Arid zone taxa such as *C. pleiocephala* and *C. chrysantha* (Schdl.) Benth. certainly have a superficial

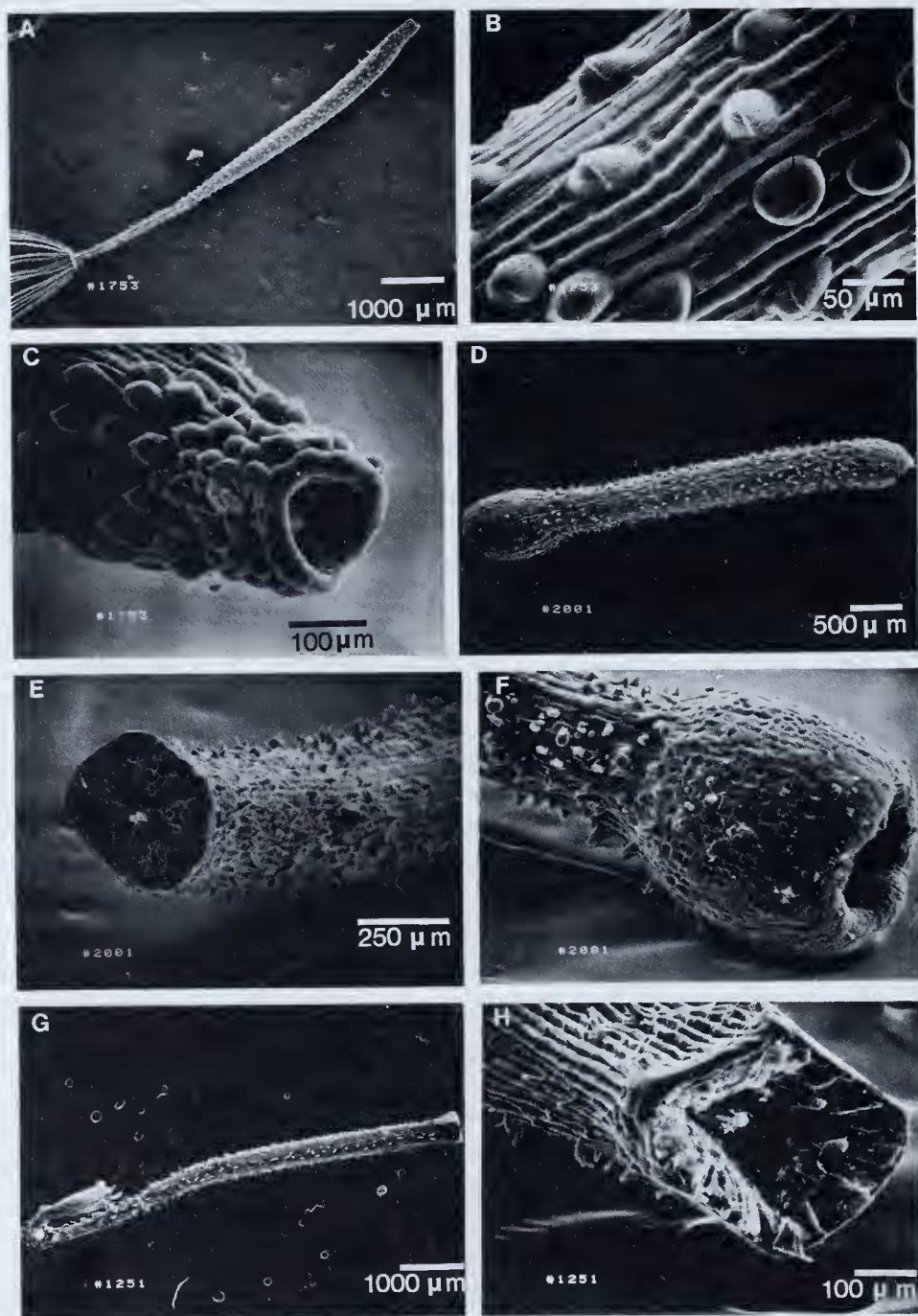


Fig. 4. Surface features of fruit. a,b,c — *Millotia tenuifolia*, general view, myxogenic papillae and carpodium (Short 1753). d,e,f — *Scyphocoronis incurva*, general view, base lacking carpodium and hollow apex (Short 2001). g,h — *Toxanthes muelleri*, general view (corolla attached) and carpodium (Short 1251).

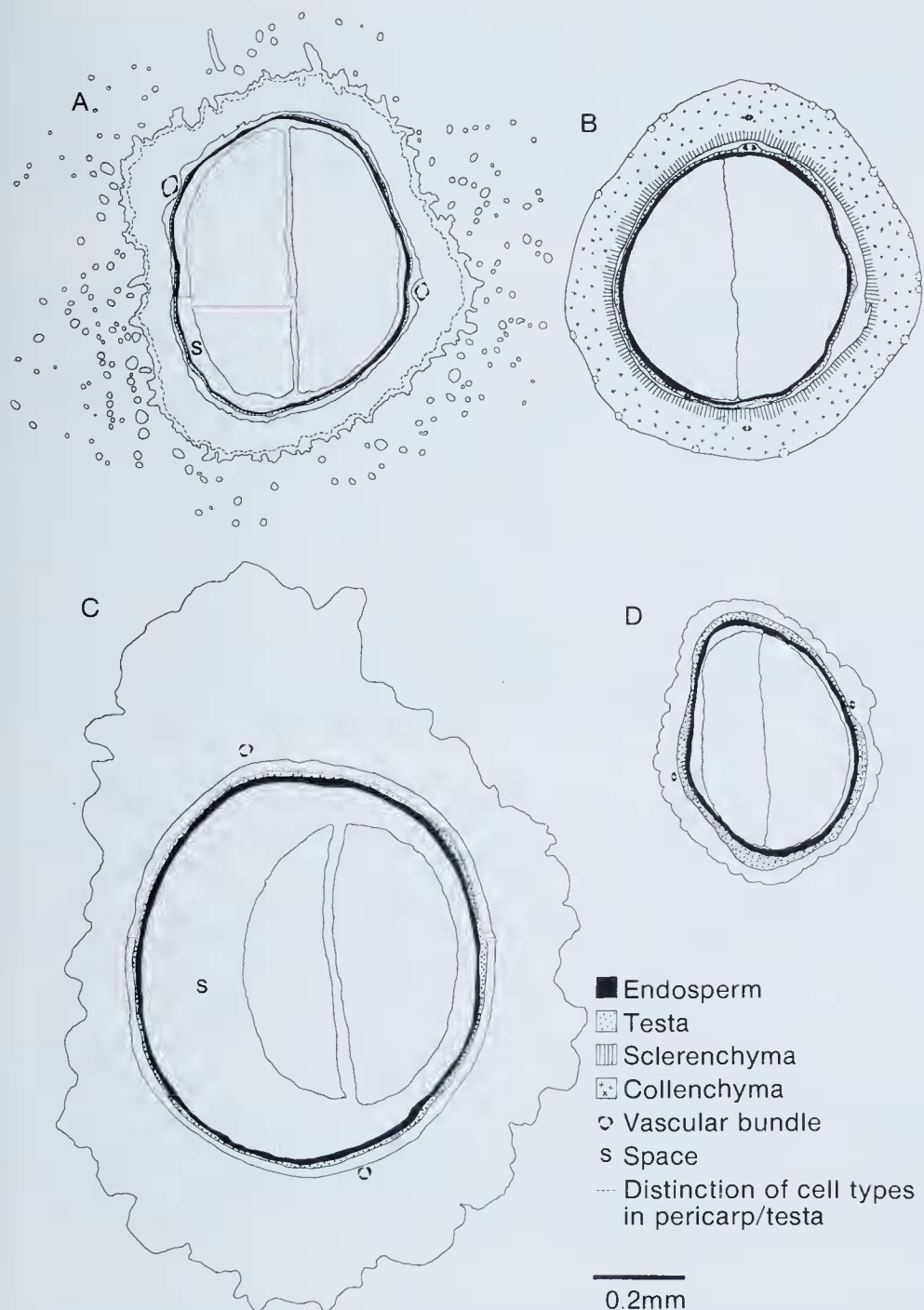


Fig. 5. Transverse sections of fruit. a — *Craspedia* aff. *pleiocephala* (Short 837). b — *Helichrysum bracteatum* (Short 3022). c — *Cephalosorus carpesioides* (Short 2403). d — *Actinobole condensatum* (Short 1005).

resemblance to *Craspedia s. str.* [which includes the many, mainly alpine, species commonly referred to the *C. uniflora* and *C. glauca* (Labill.) Spreng. complexes] and all are united in *Craspedia s. lat.* by the presence of receptacular scales. However, cytological evidence and that presented above does not support the current circumscription of the genus. *Craspedia pleiocephala* has a haploid chromosome number of $n = 6$ (Short 1981, 1986b) whereas members of *Craspedia s. str.* have a base number of $x = 11$ (Turner 1970; Beuzenberg & Hair 1984). The observed differences in the fruit are certainly major, with the largely crystalline pericarp seen in *C. aff. pleiocephala* not being observed in any of the other genera examined.

HELICHRYSUM Miller (TS)

Helichrysum, in the broad sense, occurs in Eurasia, Africa, Madagascar, Australia and New Zealand and contains about 500 species (Merxmüller *et al.* 1977). The artificiality of the genus is widely recognized, with Bentham (1867, p. 162) noting that 'the limits to be assigned to the group are very uncertain, as it is connected with so many others by insensible gradations'. Using features such as habit, shape of the involucre and receptacle, bract morphology, pappus structure, and vestiture of the cypsela, Bentham (*l.c.*) erected six Sections to accommodate Australian species of *Helichrysum*. Given the array of morphological variation exhibited there seems no doubt that in years to come most, in fact probably all, Australian species currently placed in *Helichrysum* will be referred to a number of segregate genera, e.g. *Chrysocephalum* Walp. and *Lawrencella* Lindley. Only four species of *Helichrysum* were examined in this study but observations of fruit anatomy support this contention.

Helichrysum apiculatum, a name applied to a large number of taxa deserving specific recognition, was referred by Bentham to Sect. *Chrysocephalum* (Walp.) Benth. Fruit of the taxon examined displayed a thin pericarp with two, oblique vascular bundles (Fig. 11f). Thick-walled tissue was absent from the pericarp and testa, and vascular bundles were not observed in the testa. There is a prominent, annular carpodium.

Helichrysum bracteatum in Sect. *Xerochlaena* Benth., is another polymorphic species. The fruit examined have a pericarp which is 14–15 cells wide and primarily consists of collenchyma, but there is a gradation to sclerenchyma, with the innermost 3–5 cell wide layer being solely of the latter tissue. Two lateral vascular bundles occur in the pericarp and two more occur in the testa (Fig. 5b).

Helichrysum leucopsideum, also placed by Bentham in Sect. *Xerochlaena*, has a 4–8 cell wide collenchymatous pericarp (Figs 7a, 11b). Sclerenchyma is absent. As with *H. bracteatum* this species has two vascular bundles in the pericarp, but they have a medial, not a lateral orientation. A single vascular bundle was observed in the testa.

Helichrysum cassinianum was referred by Steetz (1845) to *Schoenia* Steetz and this was followed by Bentham (1867). Haegi (1986) referred it to Sect. *Lawrencella* (Lindley) Benth. of *Helichrysum*, commenting that 'further studies are likely to confirm the placement of all these related species in a distinct genus *Lawrencella* Lindley' (p. 1526). The large, coarsely silky, compressed fruit readily distinguish it from other species examined, but it has similarities with *H. leucopsideum* in that there are two medial vascular bundles and a layer of collenchyma (2–4 cells wide) in the pericarp. Unlike *H. leucopsideum* two vascular bundles were seen in the testa (Figs 6, 11g).

HELIPTERUM DC. (TS, SEM)

Despite its illegitimacy the generic name *Helipterum* DC. is commonly applied to about 100 species from Africa and Australia. As with *Helichrysum* it is well known to be an unnatural genus (e.g. Short 1983, Wilson 1987), a fact underlined by our examination of the fruit anatomy of 11 Australian species.

The fruit section of *H. albicans* subsp. *albicans* var. *buffaloensis* is markedly different from that obtained for other species of *Helipterum*. It has two layers, each one-cell wide, of sclerenchyma and two, lateral vascular bundles in the pericarp (Figs

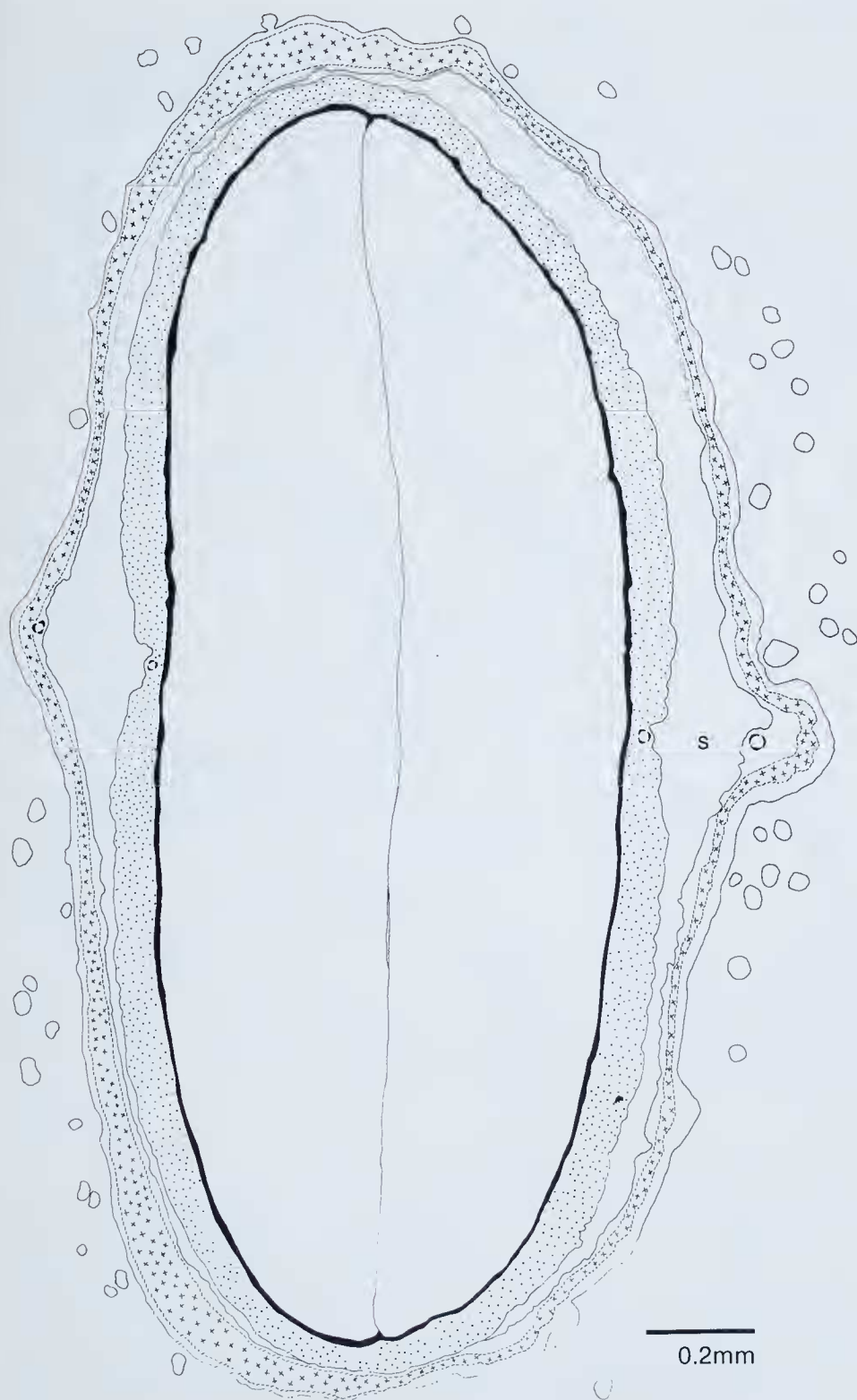


Fig. 6. Transverse section of fruit of *Helichrysum cassinianum* (Short 1575).

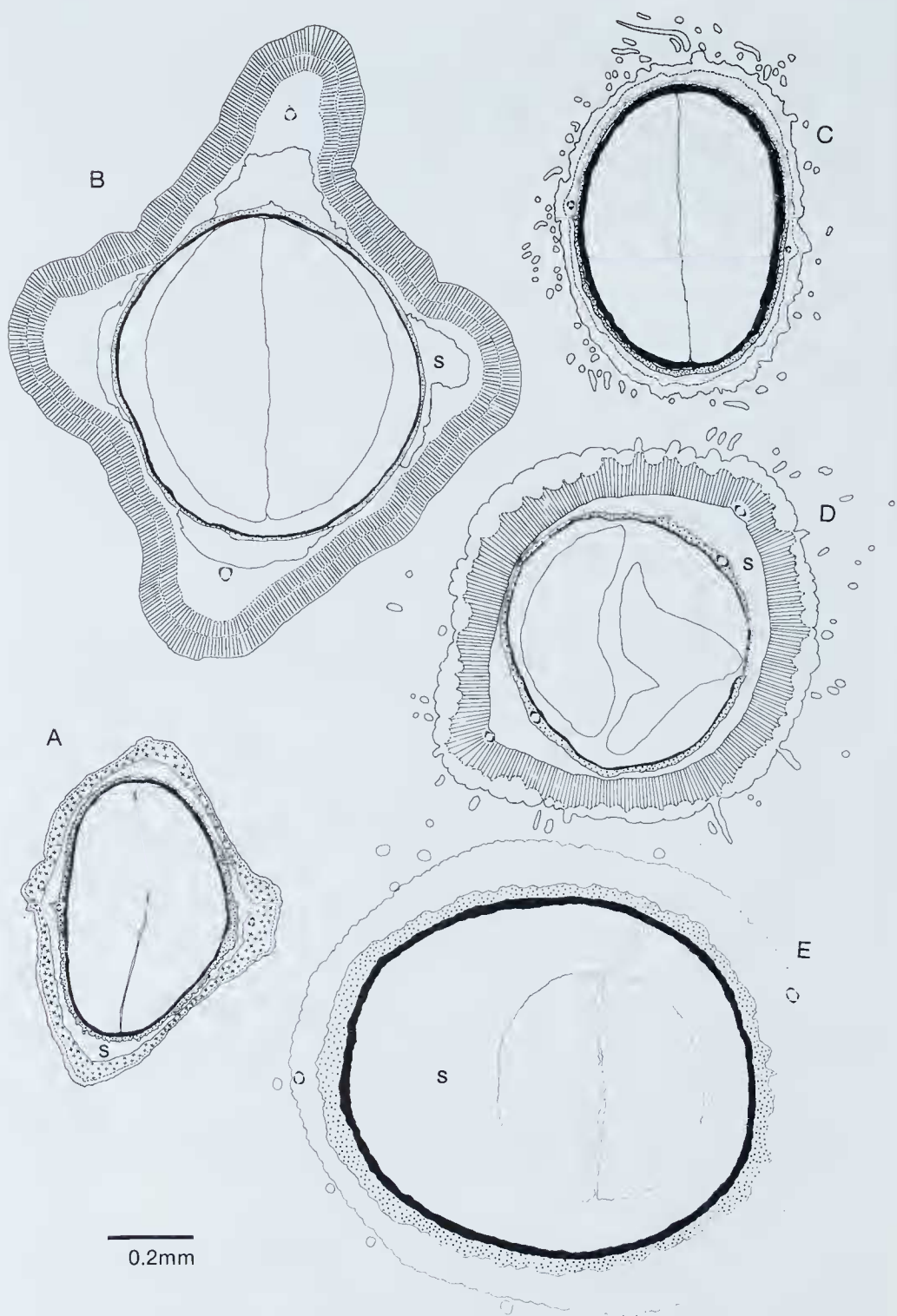


Fig. 7. Transverse sections of fruit. a — *Helichrysum leucopsideum* (Short 1554). b — *Helipterum albicans* subsp. *albicans* var. *buffaloensis* (Short 1403). c — *Helipterum pygmaeum* (Short 2973). d — *Helipterum charsleyae* (Short 2003).

7b, 11c). Vascular bundles were not observed in the testa. The *H. albicans* species group, revised by Wilson (1960), is undoubtedly generically distinct from other species currently included in *Helipterum*.

Helipterum charsleyae is also one of several species which probably constitute a distinct genus (Short 1989). Unlike other species examined it has a layer of sclerenchyma, 4–6 cells wide, in the pericarp. There are two vascular bundles in both the pericarp and testa (Fig. 7d). The fruit has a prominent carpodium and is enveloped in long trichomes with bifid apices (Figs 3e, f).

Pericarps of fruit of the remaining nine species examined lack at least a complete layer of collenchyma or sclerenchyma, but in *H. pygmaeum* there is a scattering of thick-walled cells (not depicted in Fig. 7c) in what appears to be the inner layer of the pericarp. However, in this species and *H. microglossum*, *H. strictum* and *H. uniflorum* the distinction between testa and pericarp was not obvious in TS of mature fruit. Species differ from one another in characters such as the number of vascular bundles in the testa, the vestiture of the cypsela and the presence or absence of lateral thickening of the cell walls in the epidermis (Fig. 11e; see table 1).

IXIOLAENA Benth. (TS)

Bentham (1837), when describing the new genus *Ixiolaena*, recognized a single species, *I. viscosa* Benth. Subsequently he referred a further four species, i.e. *I. brevicompta*, *I. leptolepis*, *I. supina* and *I. tomentosa* to the genus (Bentham 1867). Moore (1903) described a further species, *I. websteri*, and recently Haegi (1986) described *I. chloroleuca* and *I. pluriseta*.

Specimens of *I. websteri* and *I. pluriseta* have not been seen, but studies of the other species currently included in the genus suggest that *Ixiolaena s. str.* includes only *I. viscosa*. The habit, the presence of white laminae on the middle bracts of the involucre, and the lower petiolate leaves set this species apart from all others. Fruit of *I. viscosa* also differ from those described below in that they are not angular, are brown-black and have prominent, elongate papillae scattered over much of the surface. This species is also restricted to the comparatively high rainfall areas of south-western Australia, its supposed congeners are primarily species of eremaeon Australia. *Ixiolaena websteri* is apparently a rhizomatous, branched shrub and has female as well as bisexual forets (Grieve & Blackall 1975; Moore *l.c.*) suggesting it is not closely related to other species currently included in *Ixiolaena*. A number of inflorescence, fruit, and vegetative characters suggest that the remaining species form a natural group, to which a further species, *Leptorhynchos panaetioides* (DC.) Benth. shows affinities.

Fruit of four species, *I. brevicompta*, *I. chloroleuca*, *I. leptolepis* and *I. tomentosa* have been examined (Figs 8a–d, 11i). In many ways the cypselae of each species are very similar. All are brown, more or less oblong and have three to five somewhat obscure to prominent longitudinal ribs. An annular carpodium occurs in all species, although in *I. chloroleuca* it is almost obscured by basal, myxogenic cells. In transverse section the pericarp displays an outer sclerenchymatous layer and has two vascular bundles. A single vascular bundle was noted in the testa, and the outer one-cell wide layer of the testa consists of cells with pronounced, more or less, U-shaped thickening (Fig. 11i).

The fruit of the aforementioned species differ from each other in a number of ways, including the prominence of the ribbing, vestiture, and the position of the vascular bundles in the pericarp. *I. brevicompta* has several attributes which set it apart from the others. The cypselae of this species has a vestiture of glandular hairs on the upper c. $\frac{1}{3}$ of the body. Other species have glabrous fruit or only a few glandular hairs at the apex. The vascular bundles of the pericarp are more or less in the lateral position, not the medial position as occurs in *I. chloroleuca* and *I. tomentosa*. (Their position could not be determined in *I. leptolepis*.) *I. brevicompta* also lacks, or has very few, two-celled myxogenic cells embedded in the sclerenchymatous epidermal layer of the pericarp. Such cells are common in the other species. Although obvious in transverse section their presence is not readily observed under low magnification.

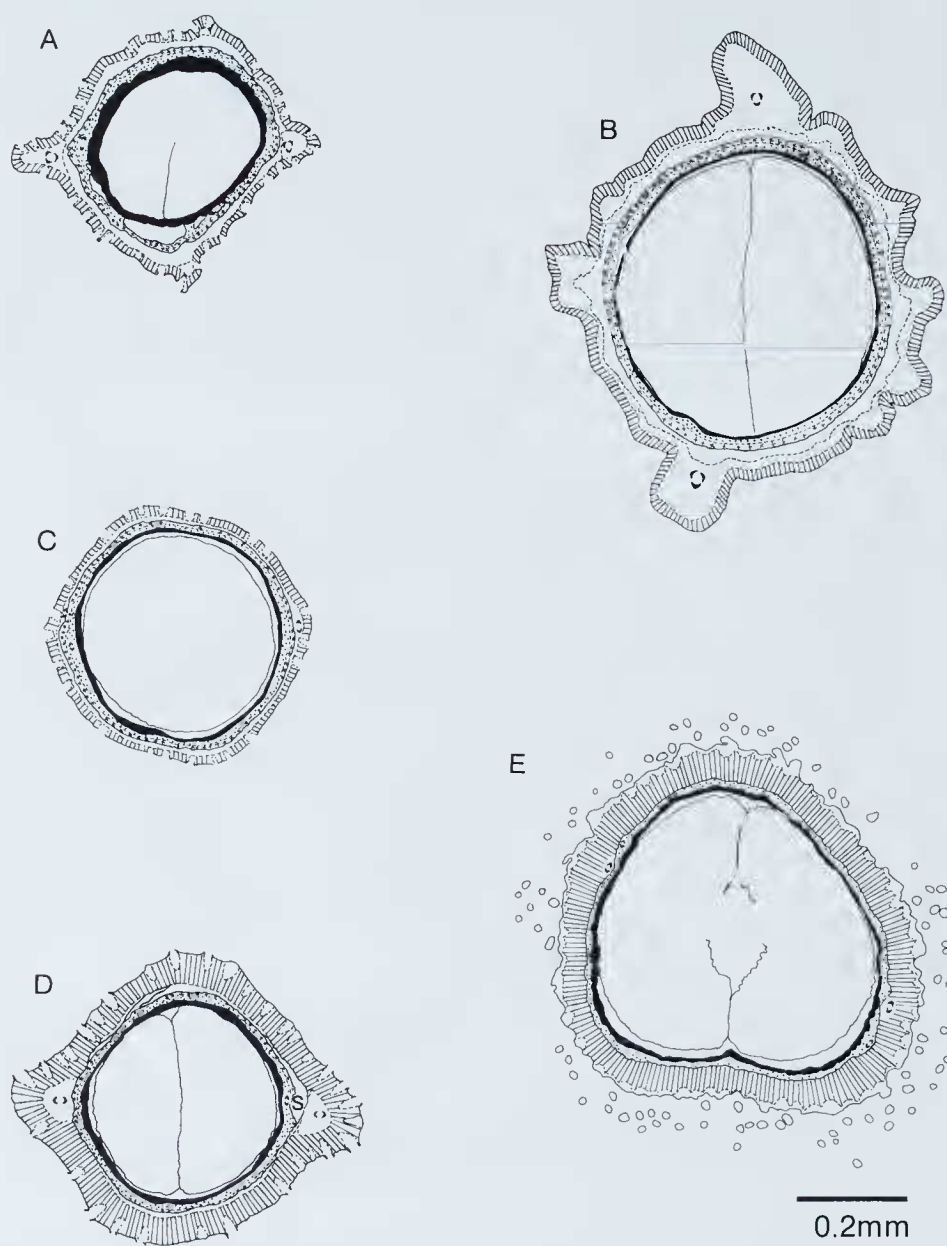


Fig. 8. Transverse sections of fruit. a — *Ixiolaena tomentosa* (Short 2988). b — *Ixiolaena brevicompta* (Short 3018). c — *Ixiolaena leptolepis* (Short 2990). d — *Ixiolaena chloroleuca* (Short 3003). e — *Myriocephalus stuartii* (Czorney 1160).

However, after soaking in water for 24 hours, fruit with these cells are found to be encased in a layer of mucilage. Despite prolonged soaking, such a layer was never evident in *I. brevicompta*. The latter species also differs from others by having the mature ovule contained in the lower $\frac{2}{3}$ of the fruit, not virtually filling the whole fruit.

Longitudinal sections of *I. brevicompta* were not obtained but the upper $\frac{1}{3}$ of the cypsela consists of sclerenchyma, i.e. it is a continuation of the outer layer of the pericarp. (If the upper part of the fruit was more narrow it would no doubt be deemed to be a 'beak' as in *Leptorhynchus*, *Millotia* etc.).

A further difference between species occurs in the width of the sclerenchymatous layer. In *I. chloroleuca* the layer is 3–4 cells wide, in other species it is only a single cell wide. The outermost layer of sclerenchymatous cells in *I. chloroleuca* is composed of much larger cells than those of the inner layers and is comparable in structure to that observed in other species.

LEPTORHYNCHOS Less. (TS)

As currently defined *Leptorhynchus* is a genus of about ten species. Transverse sections of fruit of the single species examined, *L. tetrachaetus*, reveal a pericarp which lacks a layer of sclerenchyma and has two vascular bundles which are probably in the oblique position. A further layer, probably the outer, one-cell wide layer of the testa consists of cells with U-shaped thickening. Vascular bundles were not observed in the testa. Externally the fruit is papillose and has an annular carpopodium.

Haegi (1986) noted the difficulty of distinguishing some species from groups of species in *Helichrysum* and *Waitzia* Wendl. We have noted above that *L. panaetioides* has strong affinities with many species currently placed in *Ixiolaena*.

MILLOTIA Cass., SCYPHOCORONIS A. Gray & TOXANTHES Turcz. (LS, TS, SEM)

Schodde (1963), in a revision of *Millotia*, noted a close relationship between this genus, and *Scyphocoronis* and *Toxanthus*. He reported that *S. majus* (Turcz.) Druce is almost morphologically identical to *T. muelleri* except for the hollow cup-like apex of the fruit. He further noted that an undescribed species had the habit, indumentum, and involucre of *Toxanthus*; the fruit of *Scyphocoronis*; and the alternate leaves, peduncles, floret form, free bracts and peduncles typical of some species of *Millotia*. (This species has since been named *S. incurva*.) Despite the intricacy of the relationships each genus was maintained.

Sections, both TS and LS, show a marked similarity in the fruit of species examined. All possess a layer of sclerenchyma in the pericarp (Fig. 12h). The seed is always enclosed in the lower portion of the fruit, and whether or not it tapers to a distinct beak or forms a hollow apex, the upper part of the fruit is formed of sclerenchyma, this being a continuation of the same layer of tissue surrounding the seed. Of the species examined all but *M. myosotidifolia* have only two vascular bundles in the pericarp; the latter has four.

There is some variation in two aspects, i.e. the carpopodium and the vestiture (Figs 3g–h, 4a–h). A carpopodium is best developed in species of *Millotia* and is absent or at least less well developed in *Toxanthus* and *Scyphocoronis*. However, it is not well developed in all *Millotia* species, e.g. in *M. greevesii* F. Muell. and *M. macrocarpa*. Schodde it is much less prominent than in *M. myosotidifolia*. More marked are differences in the vestiture of the fruit. Distinct, apparently two-celled, myxogenic papillae occur on the surface of species of *Millotia*. In *M. myosotidifolia* and *M. inopinata* Schodde they are particularly elongated and appressed (Fig. 3h). Papillae of this type seem to be absent from *Scyphocoronis* and *Toxanthus* but trichomes do occur over much of the fruit surface in these genera. Their structure could not be readily determined, however, at least some of the trichomes are glandular. Most importantly such glandular trichomes have been observed towards the apex of fruit of *M. greevesii*, *M. macrocarpa* and *M. tenuifolia*. They were not observed in *M. myosotidifolia*.

Unless considerable emphasis is placed on the difference in fruit vestiture then the anatomical work adds little support to Schodde's contention that the three genera be maintained.

MYRIOCEPHALUS Benth. (TS, SEM)

As previously noted (Short 1983; Wilson 1987) the genus *Myriocephalus*, as circumscribed by Benth (1867), is an unnatural group, a fact underlined by our studies of fruit anatomy of some species. *M. gracilis* differs from all other species

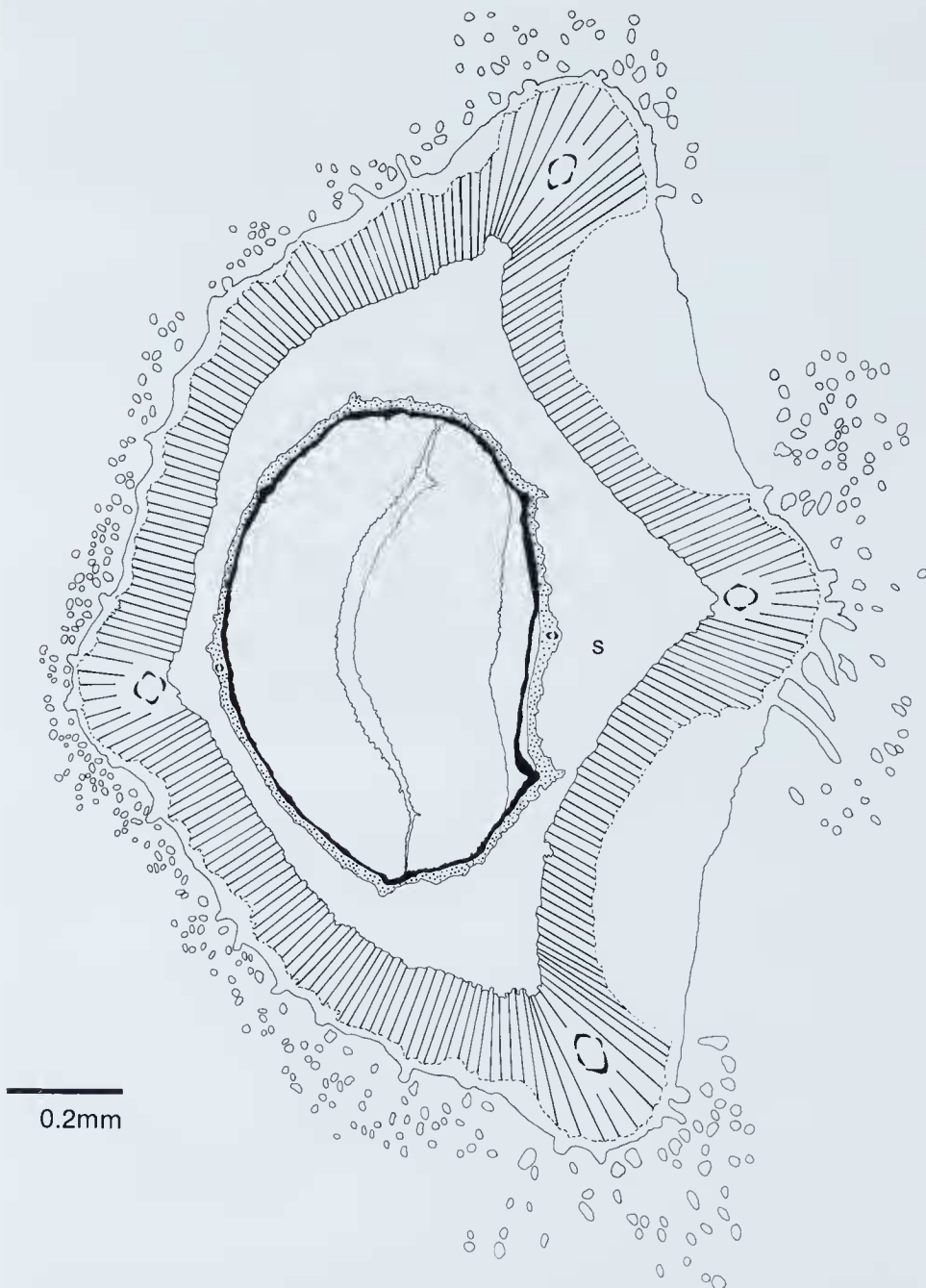


Fig. 9. Transverse section of fruit of *Myriocephalus gueriniae* (Short 540).

currently included in the genus by bract characters and fruit anatomy. The fruit is covered by a semi-transparent layer of myxogenic cells, and has two medial or oblique vascular bundles in the pericarp. A layer of sclerenchyma, observed in the pericarp of the sectioned species of *Myriocephalus*, is absent or only partially developed in the

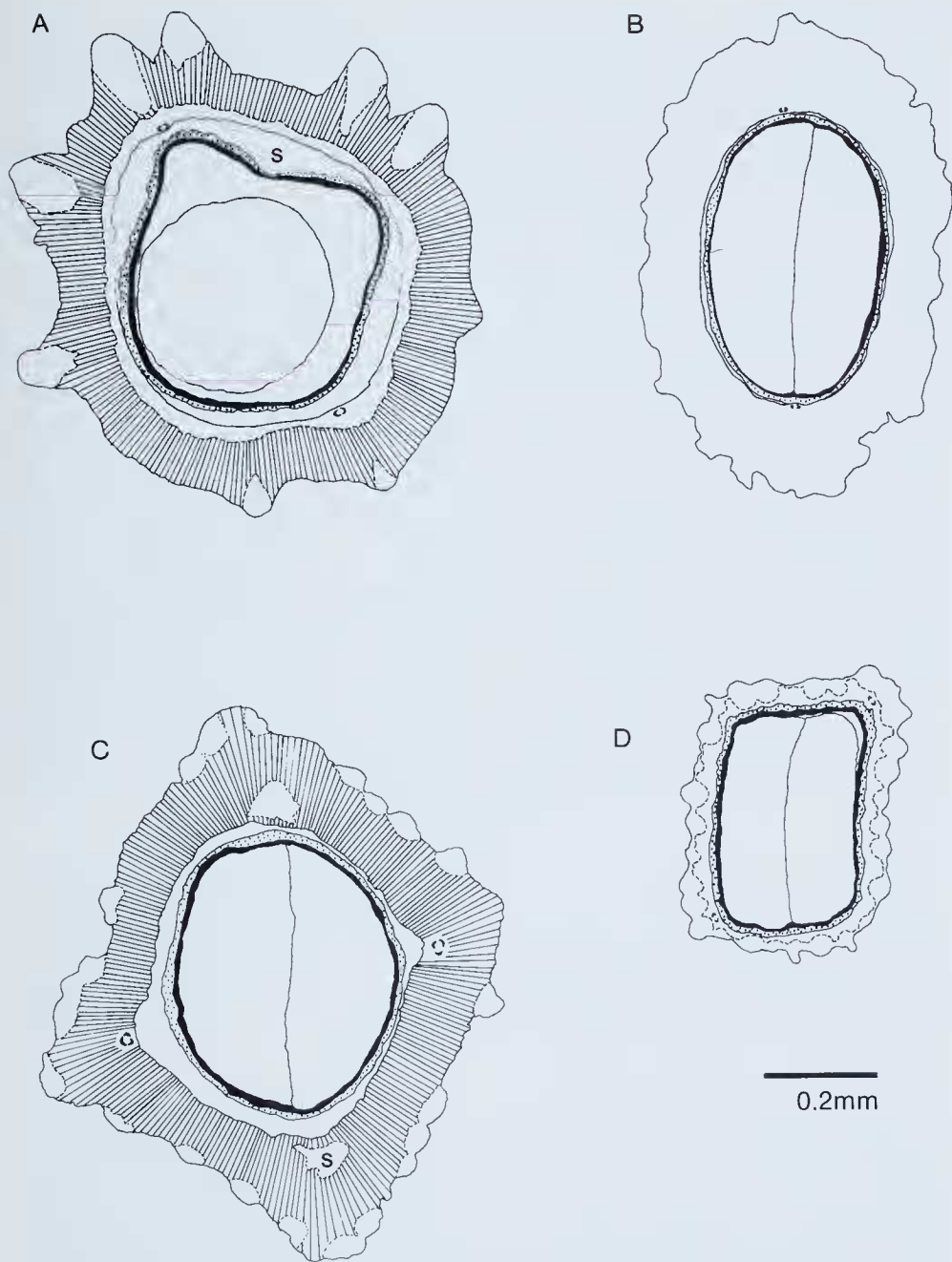


Fig. 10. Transverse sections of fruit. a — *Rutidosia helichrysoides* (Short 2999). b — *Pogonolepis stricta* (Short 2086). c — *Podolepis arachnoidea* (Willis s.n., MEL 1554024). d — *Podolepis gracilis* (Willis s.n., MEL 611247).

fruit of *M. gracilis* and seems to be part of the testa, not the pericarp. The affinities of *M. gracilis* are with species of *Helipterum* s. lat.

Myriocephalus helichrysoides A. Gray, *M. nudus*, *M. pluriflorus* (J. M. Black) D. Cooke, *M. rhizocephalus* (DC.) Benth. and *M. rudallii* (F. Muell.) Benth. plus *Gnephosis pygmaea* form a distinct group, with all species having similar fruit and

pappus characteristics. All have more or less narrow ellipsoid fruit with a sparse covering of straight twin hairs, and an annular carpopodium. A pappus is either absent or consists of a single bristle. The only species sectioned, *M. nudus* and *G. pygmaea*, display a testa with a crystalline layer, and a pericarp with a single, or mainly single, cell-wide layer of sclerenchyma (Fig. 11b) and two lateral vascular bundles. Three species, *G. pygmaeus*, *M. nudus* & *M. rhizocephalus*, have been viewed with the SEM. The fruit surface of each species displays a wave-like pattern caused by thickening in cells of the epidermis (Fig. 3d). Although showing similar fruit morphologies the species of this group have not been thoroughly examined in regard to inflorescence structure, and given the habit differences displayed by the species (e.g. compare *M. rhizocephalus* with *M. helichrysoides* they may prove to contain disparate taxa. However, it would not surprise if this group, along with *M. appendiculatus* Benth., were eventually regarded as *Myriocephalus* s. str.

Wilson (1987) suggested that a group of species, i.e. *M. stuartii*, *M. morrisonianus* Diels (conspecific with *Helipterum craspedioides* W. Fitzg.) and *M. guerinae* should be referred to *Polycalymma* F. Muell. & Sond. He noted that all had a similar inflorescence structure. Fruit of *H. craspedioides* have not been examined (MEL material on loan) but sections of *M. stuartii* and *M. guerinae* fruit were obtained (Figs 8e, 9, 12a, b). Both have fruit with a prominent carpopodium, a long silky indumentum of twin hairs, a layer of sclerenchyma in the pericarp, and two vascular bundles in the testa. However, there are major structural differences, including general size and shape, and the number of vascular bundles in the pericarp. There are four vascular bundles in the pericarp of fertile fruit of *M. guerinae* but only two occur in *M. stuartii*. [Paul Wilson (pers. comm., 1988) has recorded that only two vascular bundles occur in the unfertilized ovary of *M. guerinae*.] The most obvious difference pertains to two depressions occurring in the lower $\frac{1}{2}$ – $\frac{2}{3}$ of the flat surface of the fruit of *M. guerinae*. In sectioned fruit, these regions are seen to consist of parenchyma and, presumably as a result of infiltration, are not seen as marked depressions (Fig. 12a). These regions lack the long trichomes which otherwise envelop the fruit. The major anatomical differences between the species does not support the inclusion of *M. guerinae* with *M. stuartii* in *Polycalymma*.

PLUCHEA Cass. (TS)

Fruit of only *P. tetranthera* have been examined. Cypsela are glabrous and have a prominent annular carpopodium. Transverse sections revealed a thin pericarp, which lacks a thick-walled layer of tissue, and contains two vascular bundles in the lateral/oblique position. It was difficult to distinguish testa from pericarp, and what was believed to be testa was highly stained with cellular detail being almost obscured. Vascular bundles were not observed in the testa and cells with thickened walls also seemed to be absent from this tissue.

PODOLEPIS Labill. (TS, SEM)

Asteridea Lindley and *Podolepis* are the only inuloid genera in Australia which contain species with marginal ligulate florets. However, not all *Podolepis* species possess such florets, and despite statements to the contrary by Turner (1967) *Podolepis* is clearly an unnatural genus. Members of the genus are only loosely grouped together by virtue of their scarious bracts and the usually conspicuous outer florets of the capitulum. Close examination reveals an array of floret types (including capitula with bisexual florets only; or with ligulate, irregularly ligulate or bilabiate outer female florets as well as inner bisexual florets), bract morphologies, and habit differences. Various chromosome numbers ($n = 3, 7, 8, 9, 10, 11, 12$; Turner 1967; Henderson 1969) also occur. Variation in the morphology of both bracts and corolla suggest that *Siemssenia* Steetz [including *P. capillaris* (Steetz) Diels and *P. microcephala*] and *Panaetia* Cass. [probably comprising *Podolepis lessonii*, *P. muelleri* (Sonder) G. L. Davis, *P. davisiana* D. Cooke and *P. tepperi* (F. Muell.) D. Cooke] could be reinstated. Similarly both *P. georgii* and *P. kendallii* (F. Muell.) F. Muell. should be excluded from *Podolepis* s. str. Davis (1956) noted that both were atypical of the genus, and it has

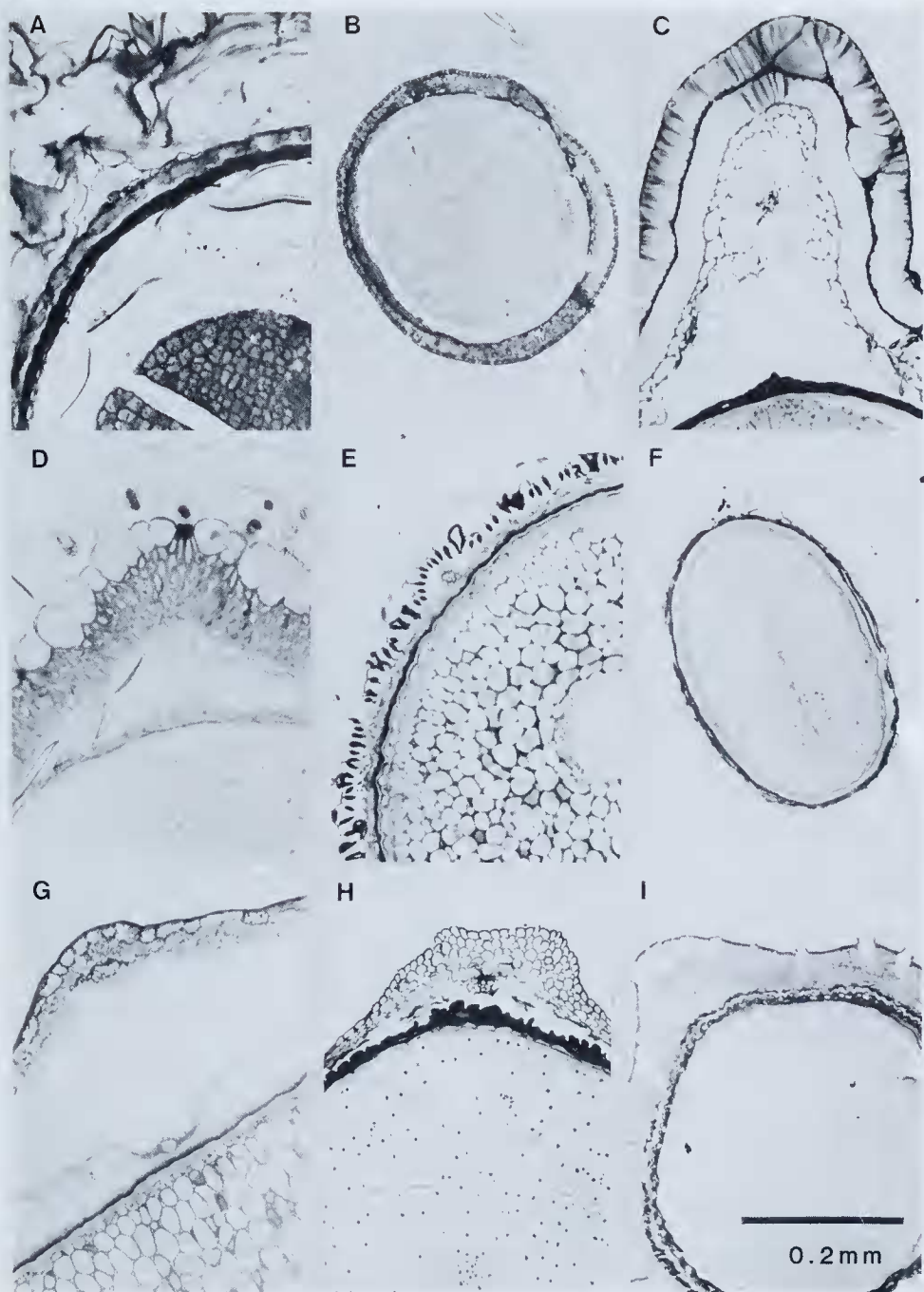


Fig. 11. Transverse sections of fruit. a — *Cephalosorus carpesioides* (Short 2403). b — *Gnephosis pygmaea* (Short 2385). c — *Helipterum albicans* subsp. *albicans* var. *buffaloensis* (Short 1403). d — *Helipterum charsleyae* (Short 2003). e — *Helipterum pygmaeum* (Short 2973). f — *Helichrysum apiculatum* (Short 3027). g — *Helichrysum cassinianum* (Short 1575). h — *Helichrysum leucopsideum* (Short 1554). i — *Ixiolaena chloroleuca* (Short 3003).

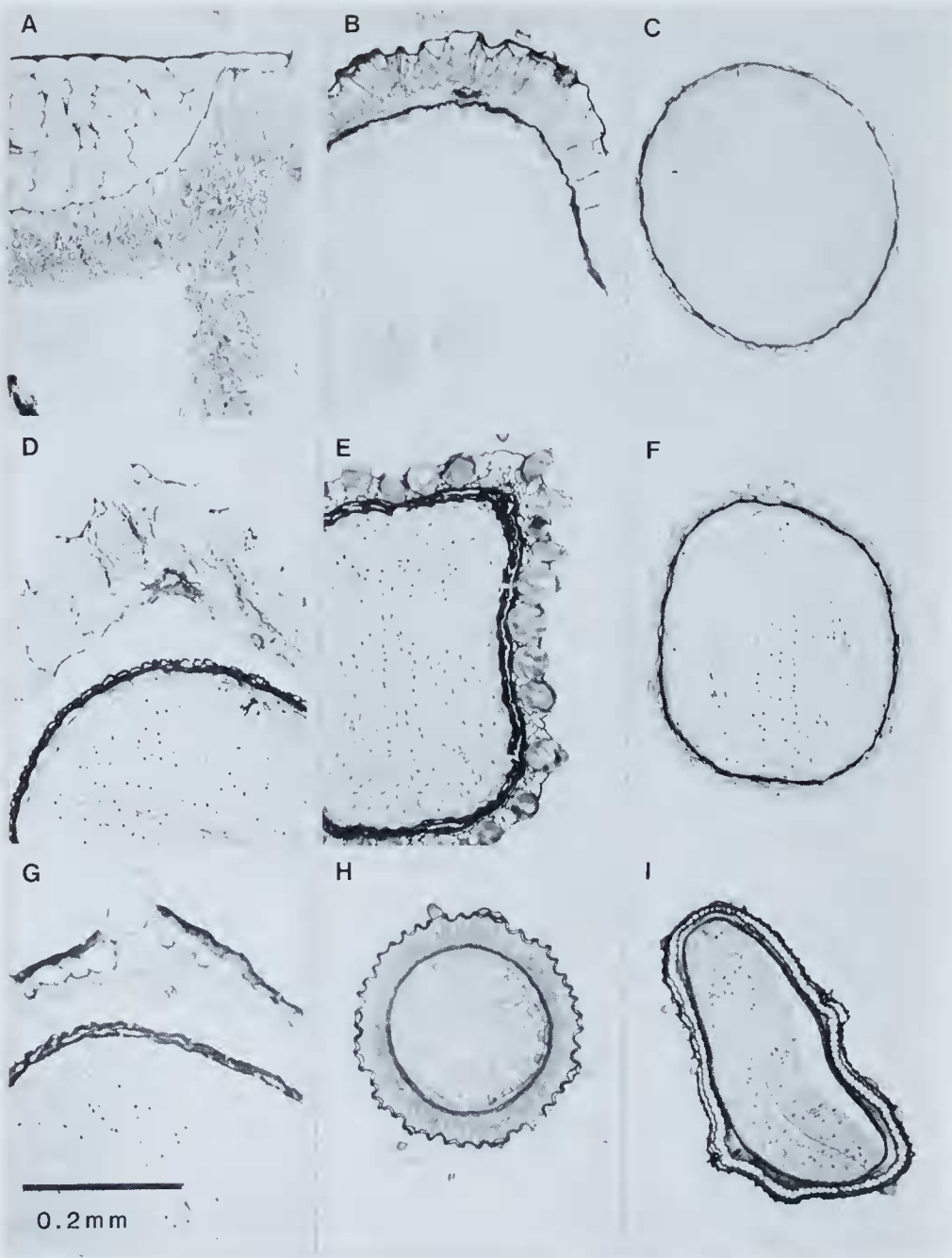


Fig. 12. Transverse sections of fruit. a — *Myriocephalus guerinae* (Short 540). b — *Myriocephalus stuartii* (Czorney 1160). c — *Pleuropappus phyllocalymmeus* (Short 841). d — *Podolepis arachnoidea* (Willis s.n., MEL 1554024). e — *Podolepis gracilis* (Willis s.n., MEL 611247). f — *Podolepis microcephala* (Short 2050). g — *Podolepis rugata* (Short 1355). h — *Toxanthes muelleri* (Short 1251). i — *Triptilodiscus pygmaeus* (Short 3014).

been noted that *P. georgi* is possibly conspecific with *Helichrysum ayersii* F. Muell. (Grieve & Blackall 1975).

Davis (*l.c.*, p. 249) stated that, with the exception of *P. kendallii* and *P. georgi*, in which the fruits are 'distinctive and diagnostic', the similarity in all other species 'is almost an occasion for comment'. Externally the pericarp of most species is somewhat similar, with the raised mucilage containing cells giving fruit a papillate appearance. A well developed carpodium is also present in most, if not all, species. However, there are internal differences, the most obvious pertaining to the presence or absence of a layer of sclerenchyma in the pericarp, and the thickness of such layers when present. Of the ten species examined *P. gardneri*, *P. gracilis* (Figs 10d, 12e), *P. lessonii* and *P. microcephala* (Fig. 12f) all lack a layer of sclerenchyma whereas *P. arachnoidea* (Figs 10c, 12d), *P. auriculata*, *P. canescens*, *P. georgi*, *P. robusta* and *P. rugata* (Fig. 12g) possess one. The orientation of the vascular bundles in the pericarp varies from medial in *P. robusta* and *P. gardneri* to almost lateral in *P. rugata*. In other species examined the orientation is oblique. (Orientation of the vascular bundles could not be determined in *P. georgi* & *P. canescens*.) With the exception of *P. georgi* vascular bundles were not observed in the testa of any species. In the latter there are two bundles within the testa, with each one being opposite a vascular bundle in the pericarp.

Although incomplete, observation of the fruit structure of species of *Podolepis* support the notion that it is an unnatural genus and that *Siemssenia* and *Panaetia* should be reinstated.

RUTIDOSIS DC. (TS)

Transverse sections of fruit of only a single species, *R. helichrysoides*, the type of the genus have been obtained (Fig. 10a). This species has an external layer of sclerenchyma in the pericarp, the layer being usually two, but sometimes three or four cells wide. Two vascular bundles (their position not determined) occur in the pericarp, but bundles were not observed in the testa. Little cell detail could be discerned in a narrow, highly stained testa but thick-walled cells seemed to be absent. Externally the cypselae are covered with two-celled papillae which have their bases in the sclerenchymatous tissue. There is a prominent carpodium.

The species of *Rutidosia* display an array of vegetative and inflorescence characters which suggest that the genus is heterogeneous. Haegi (1986) retained *R. multiflora* (Nees) Robinson in *Rutidosia* but indicated that were it not for the similar fruit it would have been excluded. Fruit of the former species and *R. helichrysoides* are similar in that both are obliquely attached to the corolla tube but an apparent absence of a carpodium has been noted in *R. multiflora*. If a carpodium is present then it is extremely small and concealed by basal papillae. The presence or absence of a carpodium is frequently indicative of different genera, thus supporting the contention that *R. multiflora* should be excluded from *Rutidosia*.

TRIPTILODISCUS Turcz. (TS)

For many years *Triptilodiscus* has been included in *Helipterum* DC. The single species, *T. pygmaeus* [syn. *H. australe* (A. Gray) Druce], is readily distinguished from species of *Helipterum* by a number of features of the inflorescence and the reinstatement of the genus by Haegi (1986) is generally accepted. The fruit has two medial vascular bundles in the pericarp but, in TS, bundles were not observed in the testa. Paul Wilson (pers. comm. 1988) has recorded a single bundle in the testa. The pronounced thickening of the outer walls of the testa (Fig. 12i) in this species has not been observed in species currently included in *Helipterum*.

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APPENDIX

Species and voucher specimens from which fruit sections were obtained. All collections gathered by P. S. Short unless otherwise indicated.

Genus and species	Collection	Genus and species	Collection
ACTINOBOLE A. Gray		HYALOCHLAMYS	
<i>A. condensatum</i> (A. Gray) P. Short	1005	<i>H. globifera</i> A. Gray	1040
<i>A. drummondiana</i> P. Short	2032		
<i>A. oldfieldiana</i> P. Short	2013	IXIOLAENA Benth.	
<i>A. uliginosum</i> (A. Gray) H. Eichler	940	<i>I. brevicompta</i> F. Muell.	3018
		<i>I. chloroleuca</i> Haegi	3003
ANGIANTHUS		<i>I. leptolepis</i> (DC.) Benth.	2990
<i>A. acrohyalinus</i> Morrison	2045	<i>I. tomentosa</i> Sonder & F. Muell. ex Sond.	2988
<i>A. brachypappus</i> F. Muell.			
	Barker s.n., MEL 594984	LEMOORIA P. Short	
<i>A. conocephalus</i> (J. Black) P. Short		<i>L. bukkittii</i> (Benth.) P. Short	1761
	Batt s.n., MEL 84412		
<i>A. cunninghamii</i> (DC. Benth.		LEPTORHYNCHOS Less.	
	Oldfield s.n., MEL 84418	<i>L. tetrachaetus</i> (Schldl.) J. Black	3015
<i>A. drummondii</i> (Turcz.) Benth.	1102		
<i>A. glabratus</i> P. Short	838	MILLOTIA Cass.	
<i>A. aff. micropodioides</i> (Benth.) Benth. Haegi	2664	<i>M. myosotidifolia</i> (Benth.) Steetz	2128B
<i>A. milnei</i> Benth.	2089	<i>M. tenuifolia</i> Cass.	1753
<i>A. aff. milnei</i>	1012		
<i>A. preissianus</i> (Steetz) Benth.	842	MYRIOCEPHALUS Benth.	
<i>A. tomentosus</i> Wendl.	845	<i>M. gracilis</i> (A. Gray) Benth.	1018
		<i>M. guerinae</i> F. Muell.	540
CEPHALOSORUS A. Gray		<i>M. nudus</i> A. Gray	1004/1569
<i>C. carpesioides</i> (Turcz.) P. Short	2403	<i>M. stuartii</i> (Sonder) Benth.	Czorney 1160
CHONDROPYXIS D. Cooke		PLUCHEA Cass.	
<i>C. halophila</i> D. Cooke	Haegi 2565	<i>P. tetranthera</i> F. Muell.	3008
CRASPEDIA Forst. f.		PLEUROPAPPUS F. Muell.	
<i>C. aff. pleiocephala</i> F. Muell.	837	<i>P. phyllocalymmeus</i> F. Muell.	841
<i>C. uniflora</i> Forst. f.	853		
		PODOLEPIS Labill.	
DITHYROSTEGIA A. Gray		<i>P. arachnoidea</i> (Hook.) Druce	
<i>D. amplexicaulis</i> A. Gray	2398		Willis s.n., MEL 1554024
		<i>P. auriculata</i> DC.	2033
EPITRICHE Turcz.		<i>P. canescens</i> Cunn. ex DC.	2142
<i>E. demissus</i> (A. Gray) P. Short	2391	<i>P. gardneri</i> G. L. Davis	Smith 66/494
		<i>P. georgei</i> Diels	Nelson 1754
FITZWILLIA P. Short		<i>P. gracilis</i> (Lehm.) Grah. Willis s.n., MEL 611247	
<i>F. axilliflorus</i> (W.V. Fitzg. ex Ewart & J. White)		<i>P. lessonii</i> (Cass.) Benth.	2404
P. Short	2188	<i>P. microcephala</i> Benth.	2060
		<i>P. robusta</i> (Maiden & Betche) J. H. Willis	
GNEPHOSIS Cass.			Forbes 252
<i>G. pygmaea</i> (A. Gray) Benth.	2385	<i>P. rugata</i> Labill.	1355
HELICHRYSUM Miller		POGONOLEPIS Steetz	
<i>H. apiculatum</i> (Labill.) D. Don	3027	<i>P. muelleriana</i> (Sonder) P. Short	843
<i>H. bracteatum</i> (Vent.) Andrews	3022	<i>P. stricta</i> Steetz	2086
<i>H. cassinianum</i> Gaudich.	1575		
<i>H. leucopsidium</i> DC.	1554		
		RUTIDOSIS DC.	
HELIPTERUM DC.		<i>R. helichrysoides</i> DC.	2999
<i>H. albicans</i> (A. Cunn.) DC. subsp. <i>albicans</i> var.			
<i>buffalocensis</i> P.G. Wilson	1403	SCYPHOCORONIS A. Gray	
<i>H. charsleyae</i> F. Muell.	2003	<i>S. incurva</i> D. Cooke	2001
<i>H. chlorocephalum</i> (Turcz.) Benth.	1746		
<i>H. floribundum</i> DC.	3025	TOXANTHES Turcz.	
<i>H. maryonii</i> S. Moore	2644	<i>T. muelleri</i> (Sonder) Benth.	1251
<i>H. microglossum</i> (F. Muell. ex Benth.) Maiden & Betche	2992	<i>T. sp. aff. muelleri</i>	2353
<i>H. moschatum</i> (Cunn. ex DC.) Benth.	2985		
<i>H. pygmaeum</i> (DC.) Benth.	2973	TRIPTILODISCUS Turcz.	
<i>H. strictum</i> (Lindley) Benth.	1581	<i>T. pygmaeus</i> Turcz.	3014
<i>H. stuartianum</i> Sonder & F. Muell. ex Sonder			
	2982		
<i>H. uniflorum</i> J. Black	3002		

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